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Behavioral Ecology Vol. 15 No. 5: 742–747
doi:10.1093/beheco/arh075
Advance Access publication on June 11, 2004

Resource partitioning between sexes in the "unconventional" hermit crab, *Calcinus tubularis*

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Together with *Calcinus verrilli* from Bermuda, the Mediterranean hermit crab *C. tubularis* is unique in that it exhibits a sharp sexual dimorphism in resource use in which one sex, the male, occupies loose shells and the other, the female, occupies attached tubes. Field surveys and laboratory experiments addressed two issues that help understand male-female resource partitioning in this species. First, the value of shells as shelters differs between sexes. Shells furnish mobility to their inhabitants, but also greater opportunities to grow because they can provide larger size than can the tubes, whereas both mobility and large dimensions are crucial selective factors for the reproductive outcomes of males only. In fact, egg production seemed not to be affected by females' sedentary life and the number of eggs was not related to the female size. Second, previous shelter experience plays a role in reducing male-female competition. I found that individual crabs, once presented simultaneously with a shell and a tube, more likely selected the type of shelter that they were collected in. Then, in male-female competition experiments, pairs composed of one crab found in a shell and one crab found in a tube and offered a shell and a tube in conjunction occupied the housing in accordance to the shelter previously occupied without any influence of their sex or size. The question remains as to how, why, and when such a sexual dimorphism in the distribution of *C. tubularis* between microhabitats did occur during a hermit crab's life.
Key words: Calcinus tubularis, resource partitioning, unconventional hermit crabs. *[Behav Ecol 15:742–747 (2004)]*

The hermit crab literature reports a number of species that permanently inhabit housings other than "conventional" gastropod shells, such as sponges, bryozoans, polychaete or vermetid tubes, and cavities in corals, scaphopod and bivalve shells, pieces of bamboo or coral, barnacles, sponges, or stones (for review, see Gherardi, 1996b). Often these alternative shelters require hermit crabs to lose mobility, with profound consequences for both feeding techniques and reproductive strategies (Gherardi, 1994; Gherardi and Cassidy, 1994, 1995). And, at least in the polychaete-tube dwelling *Discorsopagurus schmitti*, a sedentary lifestyle brings more negatives than positives (Gherardi, 1996b). However, these alternative housings constitute resources for unconventional crabs, because they provide protection from both predators and sources of physical stress, occur in short supply in the habitat, and, when suitable, favor growth, survival, and fecundity (Gherardi, 1996b).

Recently, Rodrigues et al. (2000) described field distribution and shelter preferences of *Calcinus verrilli*, endemic to Bermuda, which occupies both attached vermetid and turritellid tubes and nonattached *Cerithium* shells (Markham, 1977). In this species a sexual dimorphism in resource use was observed: in the field females were found sheltering mostly in tubes (and males mostly in shells), and the preferences of the two sexes for one or the other type of shelters matched resource utilization as recorded in the field.

These results are relevant for behavioral ecologists. Although large amounts of effort have been devoted to quantifying differences in resource use between species (see Schoener, 1974), there is still relatively little quantification of resource partitioning between the two sexes. Discussions were mostly centered on sexual segregation, as in many social ungulates in which males and females often live separately and differ in their use of abiotic and biotic resources within the habitat (Bon et al., 2001). With a few exceptions (see Abrams, 1987; Asakura, 1995), this lack in the literature is also true for hermit crabs that, because their inhabited shells are discrete, easily quantified, and manipulable resources (Hazlett, 1981), have been often studied as model organisms to test ecological theories (Liszka and Underwood, 1990).

Calcinus tubularis is a rare component of shallow subtidal habitats of the Mediterranean and is occasionally found along the coasts of the Azores and Canary Islands (Zariquiey Alvarez, 1968). This species has been widely reported to inhabit attached vermetid tubes, as implicit in its specific name, but housings are also nonattached gastropod shells (Gherardi, 1990). From nonsystematic collections (Busato et al., 1998), this hermit crab seemed to share the pattern of resource use described in *C. verrilli*.

On the above premises, *C. tubularis* provides excellent subjects for studying the potential factors that underlie resource partitioning between sexes in hermit crabs. My first goal here was to describe the field distribution of sexes between shells and tubes; then I assessed the size of these two types of housing that are adequate for each crab sex and dimension and analyzed crabs' preferences for either adequate shells or adequate tubes, as well as male-female competition on them under laboratory conditions. Lastly, I related both preference and competition to previous housing experience.

METHODS

Collection of field data

The work was carried out during 1997–1999 in a Tyrrhenian rocky shore, Baia Domiziana, in southern Tuscany, Italy (46°26′50″ N and 11°09′00″ E). This is a 13,000-m^2 bay relatively sheltered from prevailing winds and characterized

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Received 30 November 2002; revised 20 October 2003; accepted 30 October 2003.

by one *Posidonia oceanica* reef formation. The maximum depth of the lagoon is 1.75 m, with a maximum tidal range of 0.3 m. In summer, the average surface water temperature is between 26°C (early morning) and 28°C (afternoon) (24°C–26°C on the bottom); the salinity changes daily between 40 and 45 ppt (Gherardi and Benvenuto, 2001).

In July 1997, 147 hermit crabs were collected by snorkeling, those found in tubes by using a chisel and hammer and those housed in shells or in loose tubes by hand. Individuals were immediately isolated from each other in plastic bags to prevent the occurrence of any housing exchange. In the laboratory, the inhabited gastropod was identified at the species level following the method of D'Angelo and Gargiullo (1978), and its size was measured to the nearest 0.05 mm by using vernier calipers, shells being measured for base-apex axis and tubes for opening diameters. Crabs were removed from their housing by breaking the tip of the shell or the base of the tube with a vice and gently extracting individuals by using tweezers. Sex was determined, and shield length (Markham, 1968) was measured to the nearest 0.01 mm by using a light microscope and an ocular micrometer. For each ovigerous female, I estimated both clutch size by counting eggs and the mean egg diameter (averaged among 10 randomly selected eggs).

An adequacy index (AI) was computed for crabs occupying both shells (*Pisania maculosa* shells) and tubes to evaluate how well a housing fits its occupant. This was obtained from the formula (Gherardi and Vannini, 1993), modified from Vance (1972):

$$\mathrm{AI} = 100 \times (S_{\mathrm{obs}} - S_{\mathrm{exp}})/S_{\mathrm{exp}},$$

where S_{obs} is the size of the housing actually occupied by an individual, and S_{exp} is the size of the housing which that size of crab "prefers," as given by the regression line for hermit crab length and the size of the housing chosen in the housing selection experiment as described below. An AI close to 100% means that crabs occupy in the field housings having a nearly preferred size.

Laboratory experiments

During May–September 1998 and 1999, experiments were run in the laboratory. Around 300 hermit crabs were collected as above from the study site and from adjacent areas; from these, we selected adults (i.e., individuals with clearly distinguishable gonopores), having a shield length comprised from 1.5–3 mm (that corresponded to the size classes with a larger overlap between the two sexes) and being nonovigerous if female. Hermit crabs were maintained for no more than 1 week until used in an individual 50-ml compartment in a 24-compartmented plastic tray containing natural seawater, at ambient temperature (24°C), and under a natural light/dark cycle (0600 h light on and 2000 h light off). They were fed a diet of commercial shrimp pellets every third day.

Before testing, every crab was gently removed from its housing as above described and its sex was determined. Experimental aquaria consisted of plastic bowls (diameter = 10 cm) containing 150 ml natural seawater kept at the same environmental condition as in the animal maintenance.

Three series of experiments were conducted, the first aiming at determining the optimal size of shells or tubes for each size in the two sexes of crabs (housing selection experiment). The results obtained from this experiment allowed me to define as adequate, in the size for every test crab, the housings offered in the other two series of experiments. In the free-access experiment, I analyzed the preference of the two sexes between a shell and a tube of adequate size in the absence of any potential competitor. Third, I explored the role played by interference competition on the occupation of a housing of adequate size (competition experiment) in similarly sized pairs composed of a male and a female. The effect of the previously occupied housing (either a shell or a tube) was always recorded.

As potential housings, I used empty and intact *Pisania* shells (the shells most often occupied by crabs in the study population) and empty and intact *Lementina* tubes (the unique vermetid species found in the collection site). These were prepared by collecting live gastropods from the study area, boiling and removing the flesh, rinsing in seawater, and air-drying. Housing sizes (i.e., shell length and tube opening diameter) were measured as above. Experiments ended after 24 h from their beginning, a time previous pivotal observations had shown that crabs usually ceased exploring and moving into new shelters, as well as combating between each other. The housing occupied at the end of the experiment was the datum that I later analyzed.

Twenty males and 20 females with shield length regularly spaced from 1.6–2.8 mm were used in the housing selection experiment. Hermit crabs of the two sexes were divided evenly between the two treatments, which consisted in offering every crab separately with either five shells or five tubes within a gradient of housing sizes with at least one housing shorter and one housing longer than the housing occupied in the field (shell length = 12.6–22.5 mm; tube opening diameter = 3.8–7.9 mm). Hermit crabs originally collected in shells and in tubes were presented with shells and tubes, respectively.

In the free-access experiment, 100 naked hermit crabs (50 males and 50 females), of which 56 previously occupied a shell and 44 a tube, were presented simultaneously with one adequate shell and one adequate tube, which were placed next to each other on the substrate with their opening upward at the center of the bowl.

In the competition experiment, 96 pairs composed of a naked male and a naked female were tested in the presence of the two housings of adequate size. The two individuals were matched for shield length, the difference being less than 4% on average. A tie was declared when both hermit crabs were recorded as still naked. This experiment consisted of four conditions that differed for the housing previously occupied by the two opponents: that is, (1) both opponents from a shell, (2) both opponents from a tube, (3) the male from a shell and the female from a tube, and (4) the male from a tube and the female from a shell.

Each crab was tested once and then returned to its collection site.

Statistical analyses

G test adjusted by William's correction and binomial test (when sample sizes were less than 25) were used for the frequency data. Differences of AI between sexes and of clutch sizes for females between the two housing types were assessed by Student's *t* test. For the potential correlation between egg number and female size I used Pearson correlation test. Pearson correlation test was also applied to determine if crab size was significantly correlated with housing size, and then ANCOVA was used to test for a difference in the size of the housings selected by males and females. *P* values of less than 0.05 were considered statistically significant.

RESULTS

Resource partitioning in the field

Field surveys confirmed previous nonsystematic records (Busato et al., 1998) showing that shell-dwelling *C. tubularis* occupied *P. maculosa* shells to a greater extent (66%) than

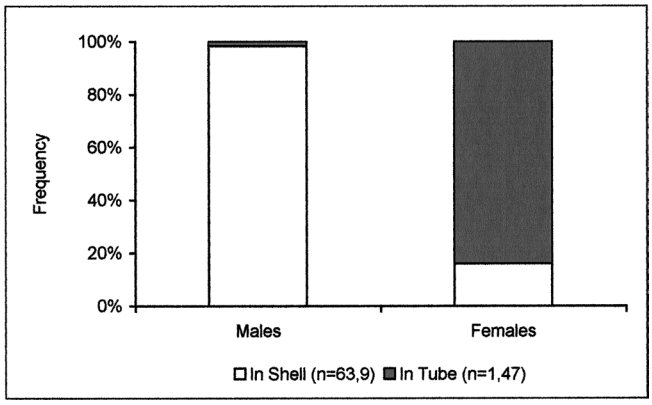

Figure 1
Field survey: distribution of males and females between loose gastropod shells (mostly *Pisania maculosa* shells) and attached vermetid tubes (exclusively *Lementina arenaria* tubes).

other gastropod species, mostly *Cerithium* spp. and *Gibbula* spp. The occupancy of these shell types reflects the availability of gastropod species within the study habitat, as already shown in the syntopic *Clibanarius erythropus* (Benvenuto and Gherardi, 2001). The inhabited tubes were exclusively produced by the vermetid *Lementina arenaria*. Twenty-seven crabs were found in loose *Lementina* tubes. These specimens were, however, excluded from the analysis because the occupied tubes could have been detached from the substrate during sampling.

Shells and tubes were sharply partitioned between sexes: more than 98% of males (i.e., 63 out of 64) were found in shells, whereas around 84% of females (i.e., 47 out of 56) occupied fixed tubes ($G_1 = 100.511$, $p < .001$) (Figure 1). The AI of *Pisania* shells averaged 60.47% (SE = 1.01, $n = 40$) for males and 44.37% (SE = 1.77, $n = 8$) for females, with a significant difference between sexes (after arcsine square-root transformation for percentages: $t_{46} = 6.607$, $p < .01$). In the females only (because only one male was found in a tube), the AI for tubes scored 92.38% (SE = 0.41, $n = 47$).

Of the 56 females collected, 73% were ovigerous. Ovigerous females found in tubes were clearly more numerous than were those found in shells (37 versus four); although sample sizes were clearly unbalanced, a tentative comparison for clutch size between the ovigerous females found in shells (215.0 ± 95.8 eggs per female, $n = 4$) and in tubes (147.6 ± 25.1 eggs per female, $n = 37$) did not reveal any significant difference ($t_{39} = 0.983$, p = ns). Nor did eggs differ in their diameter, which averaged 0.35 (±0.02) mm. No significant correlation was found between egg number and female size ($r_{39} = .195$, p = ns).

Crabs inhabiting shells had significantly longer shields than did those occupying tubes ($G_5 = 19.548$, $p < .01$), and males had significant larger dimensions than did the females ($G_5 = 12.596$, $p < .05$) (Figure 2).

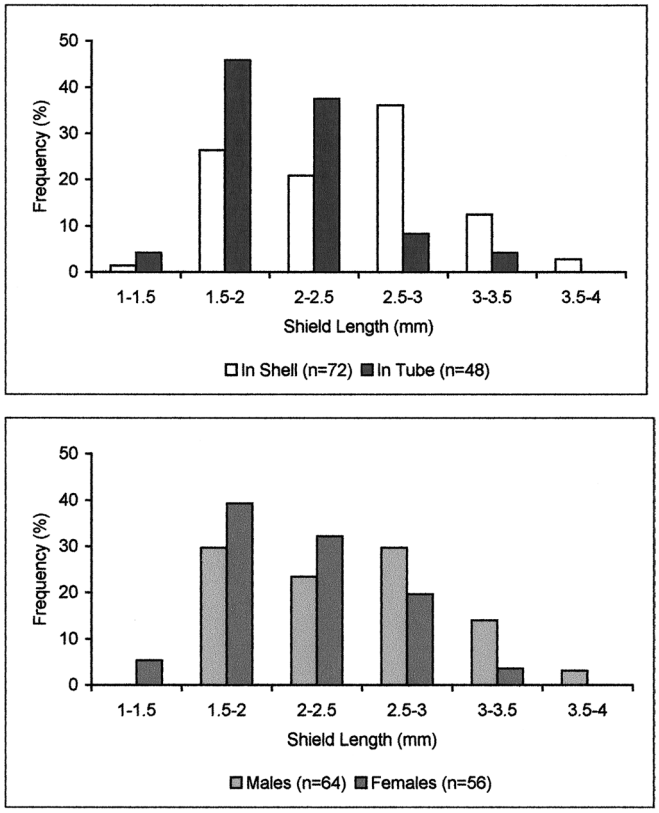

Figure 2
Field survey: size frequency distributions compared between crabs inhabiting two types of housing (either shells or tubes) (top) and sexes (bottom). Shield length is an estimate of crab size.

Housing selection experiments

Linear regression analyses showed that housing sizes were positively correlated with crab shield length for both males (shell: $r_8 = .979$, $p < .01$; tube: $r_8 = .981$, $p < .01$) and females (shell: $r_8 = .957$, $p < .01$; tube: $r_8 = .978$, $p < .01$), without any male-female difference (shell: $F_{1,17} = 4.251$; tube: $F_{1,17} = 0.987$). Regression equations (with y = housing size and x = shield length) were, in the case of males, $y = 8.41x - 1.118$ for shells and $y = 3.612x - 2.242$ for tubes, and, in the case of females, $y = 8.404x - 1.915$ for shells and $y = 3.599x - 2.352$ for tubes. These equations were used to estimate housings of adequate size for every crab tested in the free-choice and in the competition experiments.

Free-choice experiments

Forty-eight percent of the test crabs did choose a housing, the majority of them being individuals that previously inhabited a tube ($G_1 = 7.673$, $p < .01$). Restricting the analysis to those crabs that made a choice, 90% and 61% of individuals found in a shell and a tube, respectively, did choose the same type of housing as their previous one ($G_1 = 13.457$, $p < .001$). No difference was found between males and females, both sexes preferring shells when previously in a shell in the 90% of the examined cases and a tube when previously in a tube ($G_1 = 0.142$, p = ns) in 64% and 57%, respectively, of the males and the females analyzed (Figure 3). Significantly more crabs chose the type of housing they previously occupied when the latter was a shell than when it was a tube ($G_1 = 5.315$, $p < .05$).

Competition experiments

Ties mostly occurred when both individuals of the pair previously occupied a tube (42%; $G_3 = 6.438$, $p \approx .05$). In the other cases in which at least one crab was recorded in a housing at the end of the experiment (Figure 4), males won a shell when their previous housing was a shell and their opponent was a female found in both a shell (binomial test $p = .0207$) and a tube (binomial test $p = .0007$). On the other hand, more

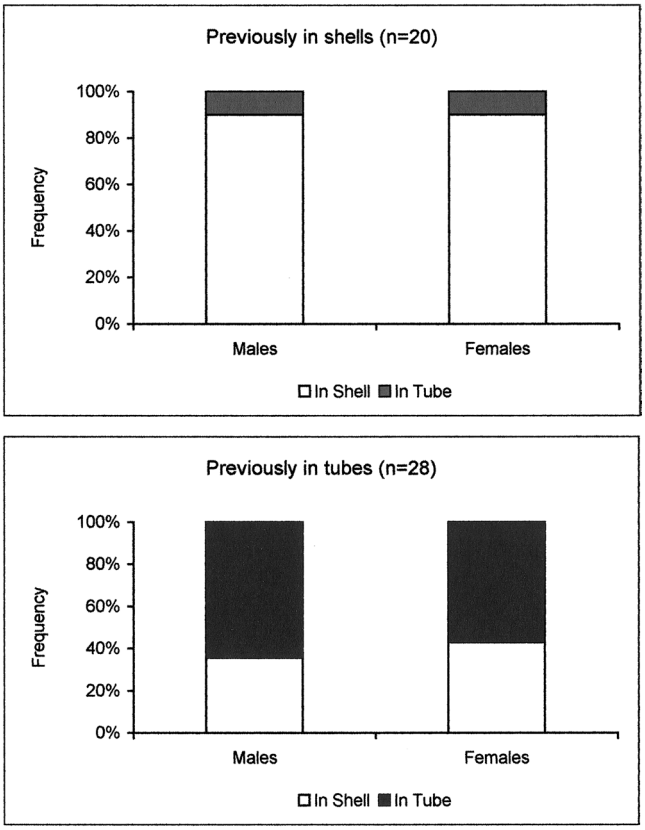

Figure 3
Free-choice experiment: distribution between two types of housing (either shells or tubes) of male and female crabs that were previously found in either shells (top) or tubes (bottom). In this experiment, each naked individual was offered one shell and one tube in conjunction for 24 h.

females won a shell when previously in a shell and opposed to a male found in a tube (binomial test $p = .0245$), whereas shell occupancy did not differ between sexes when both individuals previously occupied a tube (binomial test $p = .3953$).

DISCUSSION

Together with *C. verrilli* (Rodrigues et al., 2000), *C. tubularis* is unique in that it exhibits a sharp sexual dimorphism in the type of resources used in which one sex, the male, occupies loose shells and the other, the female, attached tubes. Although the present study was limited to the reproductive period, such resource partitioning between sexes seems to occur all year round (Gherardi F, personal observation). In other hermit crab species, sexual differences were referred to shells of different species or of different dimension categories and were mostly related to sexual dimorphism in hermit crab size (Abrams, 1987; Asakura, 1995; Bertness, 1981, 1982; Blackstone, 1985; Blackstone and Joslyn, 1984; Fotheringham, 1976).

Obvious consequences of the occupancy of either shells or tubes are several different ecological features of the two sexes. I did not have yet explored in a systematic fashion costs and benefits of *C. tubularis* tube-dwelling habit. However, a suggestion from the present study was that tubes are the least favored shelters. Crabs collected in a tube differed from those found in a shell in having a greater tendency to occupy a new housing, and even if the majority of them occupied again a tube at the end of a free-choice experiment, several selected

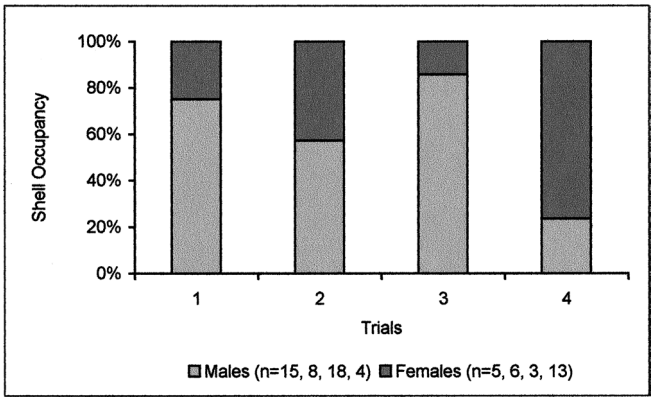

Figure 4
Competition experiment: frequency of male and female crabs that were found inhabiting shells after 24 h of cohabitation. In this experiment, male-female pairs composed of similarly sized naked individuals were offered one shell and one tube in conjunction. Trials differed for the housing that the opponents previously occupied. Trial 1 indicates both individuals in shell; trial 2, both individuals in tube; trial 3, the male in shell, the female in tube; trial 4, the male in tube, the female in shell.

a shell. Then, the occupancy of a tube seemed to reduce crab ability to conquer a new shelter when naked. On the other hand, my data showed that egg production is insensitive to the female lifestyle; in fact, clutch size and egg dimension seemed not to differ significantly between mobile and sessile individuals. Besides, the AI of tubes was not much different from 100%, suggesting that adequate tubes are not limiting for the females in the study area and/or competition to acquire them is weak.

Three factors have been advocated to be the most likely candidates to explain sexual dimorphism in resource use (Abrams, 1987), factors that, however, are not mutually exclusive alternatives. The first, the growth hypothesis, states that resource partitioning between sexes can be related to the differential availability of energy for growth. Males can devote more energy to growth because in this sex reproduction is usually less expensive than in the females. And crabs having larger sizes display a greater ability to acquire higher numbers of available shelters and higher numbers of the more preferred ones (Asakura, 1995). This hypothesis is not validated in *C. verrilli*, in which females exclusively occupy vermetid tubes, notwithstanding that they are larger than the males (Rodrigues et al., 2000). The bigger individuals in the population of *C. tubularis* were mostly males, but resource partitioning between sexes appeared sharp also in the smaller size classes. In the study area, empty shells were almost absent, and the intra- and interspecific (Busato et al., 1998) competition for them was strong, as suggested by the occupancy of shells with a relatively low AI. *C. tubularis* males displayed a superior fighting ability when opposed to the females and were collected in significantly more adequate shells than the other sex although sharing a similar preference for shell size. However, as shown in the laboratory, the competitive superiority of males seemed to be independent of their relative size.

The basic idea of the second hypothesis, the sexual selection hypothesis (Bertness, 1981), is that fitness increases more rapidly with size for males than for the females because of intrasexual competition between males to obtain matings. At least among mobile gastropod-dwelling hermit crabs, reproductive behavior involves dragging and carrying the female as a form of mate guarding (Hazlett, 1966). For *C. tubularis* males, crucial selective factors are both mobility

(which is indispensable for them to find a mate) and a large dimension (which provides them with a higher probability to win intrasexual competitions for a mate), both properties that have no effects upon the reproductive output of females; in fact, egg production seemed not to be affected by female sedentary life, and the number of eggs was not related to their size. Shells furnish to their inhabitants not only mobility but also greater opportunities to grow because they display larger size than the tubes. Thus, with the exception of the few male crabs found in a tube, males are expected to be more motivated to battle for a shell than the other sex and to escalate more readily in shell fights.

Third, a form of intersexual character displacement that originates from a competition between sexes (Slatkin, 1984) could induce sexual dimorphism in resource use even in the absence of either any inherent difference in growth potential or sexual selection. In *C. tubularis*, the experience of inhabiting a specific shelter predisposes a hermit crab to choose the same shelter; thus, experience maintains shelter displacement between sexes and ensures their peaceful coexistence. The effect of prior shelter use on future selection of the housing has been explored only in a few conventional hermit crab species (in *Calcinus laevimanus*: Reese, 1963; *Pagurus longicarpus*: Blackstone, 1984; *Pagurus bernhardus*: Elwood et al., 1979; and *P. granosimanus*: Hahn, 1998), but the results obtained in the above listed studies showed an apparent discrepancy, possibly because previous shells affect different crab species to differing degrees owing to their availability in the habitat (Hahn, 1998).

In *C. tubularis*, I found that crabs, once presented simultaneously with a shell and a tube, more likely selected the type of shelter that they were collected in. Then, in male-female competition experiments, pairs, composed of one crab found in a shell and one crab found in a tube and offered a shell and a tube in conjunction, occupied the housing according to the shelter previously occupied and without any influence of their sex or size. As a consequence, predisposition to a specific shelter type could by itself lead to lower levels of interference competition between sexes.

As regards to the mechanisms by which preferences for the shelters previously used could arise, Elwood et al. (1979) suggested that crabs may learn the various aspects of a particular shelter while in occupation and subsequently seek those characteristics that have been beneficial to them in the past. Particularly in the case of unconventional crabs, it seems possible that after ecdysis the crab becomes molded by the housing in which it is living to a particular shape and thus comes to prefer a shelter that well-fits its body. Differences in a number of morphological characteristics that were directly affected by the inhabited shelter were only shown in *Pagurus bernhardus* living in *Dentalium* shells (Selbie, 1921), in *D. schmitti* living in *Sabellaria* tubes (Gherardi and McLaughlin, 1995), and especially in *C. verrilli* living in gastropod tubes (Rodrigues et al., 2002).

Conclusions

The present study has addressed two issues that help understand resource partitioning between sexes in the unconventional hermit crab *C. tubularis*. The first was that the value of shells as shelters differs between sexes. In addition, previous housing experience was shown to play a role in reducing male-female competition.

The ontogeny of the sharp intersexual segregation between shells and tubes is still puzzling; the question remains as to how, why, and when such a sexual dimorphism in distribution between microhabitats did occur during the history of individual crabs (Gherardi, 1996a).

My warmest thanks are directed to Patrizia Busato and other students who carefully conducted a part of the field work. Funds were provided by MIUR.

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